— (1965): Besonderheiten an Cavicornier-Hörnern. Milu 2, 21-47.

NAAKTGEBOREN, C., und VANDENDRIESSCHE, W. (1962): Beiträge zur vergleichenden Geburtskunde I. Z. Säugetierkunde 27, 83—110.

PETZOLD, G. (1963): Geburt im Tierpark. Wissenschaft und Fortschritt 13, 540-541.

Petzold, H.-G. (1965): Im Tierpark Berlin 1961 erstmalig gehaltene Tierformen. Milu 2, 68-107.

PETZSCH, H. (1959): Zwei Geweihe bei einem Isubrahirsch- dinnerhalb eines Jahres. Zool. Garten (NF) 24, 517—518.

Prell, H. (1939): Tragzeiten von Cerviden. Zool. Garten (NF) 11, 182-186.

Seitz, A. (1966): Beitrag zur Haltung des Hausrentieres (Rangifer tarandus L.). Zool. Garten (NF) 33, 55-64.

Simcox, A. H. A. (1905): Breeding seasons of big game in India. Journal of the Bombay Natural History Society 16, No. 2, 370—371. SLIJPER, E. J. (1960): Die Geburt der Säugetiere. Kükenthals Handbuch der Zoologie 8

(25. Lfg.). Walter de Gruyter & Co., Berlin.

ULLRICH, W. (1961): Zweimalige Geweihbildung im Jahresablauf bei einem Rehbock. Zool.

ULLRICH, W. (1961): Zweimalige Geweihbildung im Jahresablauf bei einem Rehbock. Zool. Garten (NF) 25, 411—412. Voracek, CH. R. (1962): The White-Tail Deer (Odocoileus virginianus). Zoo News (Cleve-

land) 2, No. 6, 10—12. Voss, G. (1965): Zwillingsgeburt beim Großohr-Hirsch, Odocoileus hemionus Raf. Z. Säuge-

tierkunde 30, 20—24. Zuckerman, S. (1953): The breeding seasons of mammals in captivity. Proc. zool. Soc. London 122, 827—950.

Anschrift des Verfassers: Dr. Dieter Lau, Tierpark Berlin, x 1136 Berlin-Friedrichsfelde, Am Tierpark 41

Distribution and Population Structure of Black Rhinoceros (Diceros bicornis L.) in the Lake Kariba basin¹

By Harald H. Roth and Graham Child

Eingang des Ms. 2. 10. 1967

The damming of the Zambezi River at Kariba on 2 December 1958, led to the inundation of 2,109 sq. miles (5,462 km²) by the time the lake filled in 1963. During the course of flooding, numerous temporary and permanent islands formed on which more than 5,000 large mammals, including a population of Black rhinoceros (*Diceros bicornis* L.) became marooned. To alleviate the plight of these animals the then Northern and Southern Rhodesian Governments promoted game rescue units to remove as many of them as possible to the safety of the mainland. Physical capture methods were used for most species excluding the rhinoceros which had to be rescued individually with the aid of immobilizing drugs. Either a paralyzing or a narcotizing drug mixture was administered with a Palmer Cap Chur gun or a cross bow. The immobilized rhinos were tied up and transported to a raft on a manhandled sleigh. Before being released on the mainland each rhino was marked for future recognition, and measurement, blood and other samples were taken. Thus rescue operations offered a unique opportunity for recording

¹ Presented in abbreviated form at the Symposium on African Mammals, 26—28 September 1963, Salisbury

the size, local density and structure of the rhinoceros population over a large and sparsely settled area in the Central Zambezi Valley (Fig. 4).

The immobilization techniques have been described by Harthoorn and Lock (1960) as well as by Child and Fothergill (1962), and it remains only to mention the overall success rate of rhino translocation under the difficult conditions on Lake Kariba. With the paralyzing method (Gallamine triethiodide) which was used until early 1962 seven rhino out of twenty-five were lost while being rescued, of which one animal drowned while immobilized and another was accidentally overdosed. Narcotization with a mixture of Morphine, Hyoscine and Chlorpromazine (Largactil) as recommended by Harthoorn and Player (1962) and Harthoorn (1962) proved more satisfactory and yielded a survival rate of 90%; only three of twenty-two rhino died and of these one drowned after having been darted. In some cases Chlorpromazine was replaced by Phencyclidine (Sernyl) which did not, however, produce the favourable effects described by Harthoorn (1962) for White Rhinoceros (Ceratotherium simum Burchell). The necessity for estimating the weight of each individual rhino within fairly accurate limits, in order to calculate the required dose of the drug, was of particular significance for this study.

To allow such estimates experience had to be gained in concluding weights from the body size. For this purpose five individuals of different sizes were weighed and the growth rate of two known age animals was recorded over a period of three years (ROTH unpublished).

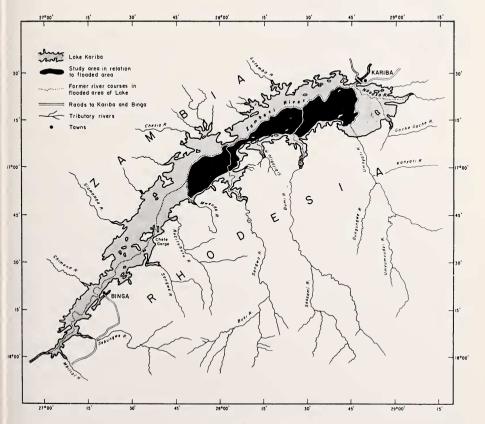


Fig. 1. Study Area in the Lake Kariba basin

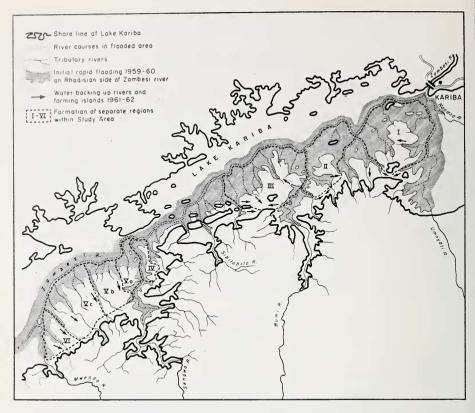


Fig. 2. Flooding of Study Area 1958-1960 and formation of regions

Area of Study

Rhino only became marooned on islands in Rhodesian waters between the Mwenda and Umniati rivers, and this area of about 484 sq. miles (1,254 km²), or roughly a fifth of the total Lake basin, is taken as the Study Area (Fig. 1).

According to the records of the Zambian Game and Fisheries Department (ANSELL 1959, 1960) relic rhino populations do occur on the northern side of the Central Zambezi Valley, but were beyond the area influenced by the flooding of Lake Kariba. In Rhodesia rhino occur throughout the Central Zambezi drainage (CHILD and SAVORY 1964, ROTH 1967), but west of the Mwenda river and east of the Umniati river they were not marooned on islands in the Lake. In these areas they had not apparently inhabited the close vicinity of the Zambezi river because of the dense Tonga settlement in the valley west of the Mwenda, and past Tsetse Control hunting operations east of the Umniati river (Fig. 3).

The Study Area was readily divisible into distinct regions separated by tributaries of the Zambezi. This separation took place early during lake formation, as water backed up the rivers rapidly. Within 9 months of the damming of the Zambezi the water level rose from 1,300 to 1,475 feet and formed six major regions (Fig. 2). Large parts of these were then inundated rather slowly during the subsequent years 1959/60 and 1960/61 as the water level rose to 1,549 feet. In each region a complex of islands formed on which rhino became marooned and had to be removed before June 1963.

The movements of marked rhino at Kariba and other observations have shown that the habits of the black rhino are generally very localized in Rhodesia (Child [1965]). During the flooding of the Kariba basin it was found that rhino were only capable of swimming very short distances and seldom entered the water except to evade capture; only one rhino was known to wade through shallow water to the safety of the mainland. From this it seemed extremely unlikely that Black rhinoceros would voluntarily cross streams or flooded valleys. Taking these facts into account, and by reference to detailed contour maps it was possible to determine roughly the area from which the captured rhinos had originated and thus to establish population densities for distinct areas within the regions studied.

Furthermore, frequent patrolling of islands in areas being flooded made it certain that all rhinoceros which drowned or died otherwise were noted in addition to those captured. It is therefore justifiable to conclude that the total number of rhino recorded in this study represented the true population figure. It was only in certain flat areas along the present shore that spoor suggested a few individuals may have withdrown onto the mainland from their original home range before being trapped by the rising waters. A careful consideration of each area showed that the number of these animals was not higher than 10–15 % of the total recorded. This percentage has been included in the calculation of maximum population density.

Distribution and Abundance

A total of 62 rhino were found in the Study Area where they had been distributed over roughly 321 sq. miles (831 km²). Two large sections between regions, totalling 63 sq. miles and roughly 100 sq. miles in regions I, II, IV and VI were apparently uninhabited by rhino (Fig. 3). Table 1 shows the number of rhino in the different regions of the Study Area in relation to their acreage. The greatest local density was found in a section west of the Sengwa river (region V), where there was one rhino per 2,200–2,600 acres (3.4–4.1 sq. miles or 8.9–10.5 km²). An the Umniati West region (I) the density was considerably less with one rhino per 3,000–3,700 acres (4.7–5.8 sq. miles or 12.1–15.0 km²). The theoretic mean density over the whole area was about one rhino per 4,350–5,000 acres (6.8–7.8 sq. miles or 17.6–20.2 km²), but considering only the area which was actually inhabited by rhino the average density figure may be increased to one animal per 2,900–3,400 acres (4.5–5.3 sq. miles or 11.7–13.7 km²).

These figures show that the abundance of rhino varied in the different areas. Possible factors influencing the abundance are the previous settlement of the Tonga people along the Zambezi, water availability and the suitability of vegetation and geological surface as rhino habitat.

1. Although most Tonga were agriculturists who hunted relatively little (SCUDDER 1962), it is quite obvious that their activities were the main reason for the difference in the abundance of rhino on the Northern and Southern Banks of the Zambezi. Between the Umniati and Mwenda rivers there were more than 13,000 Tongas on the northern bank, as compared with about 4,000 on the south bank, which, in some areas, amounted to a difference of 10:1. In contrast to the southern population, which was almost entirely restricted to the banks of the Zambezi, the settlement of the northern Tongas extended far up the tributaries and so caused far more disturbance to game. In the upper valley, beyond the Study Area, alluvial deposits on which the Tongas depended, were equally available on both sides of the river, and resulted in dense settlement on both banks. Consequently, rhino retreated some distance inland where, as already mentioned, they remained relatively abundant. Furthermore, the former Northern Rhodesian administration, now Zambia Government, in contrast to the Southern

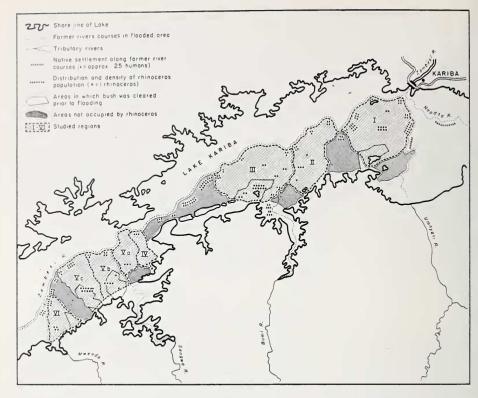


Fig. 3. Distribution of rhinoceros in relation to native settlement

Rhodesian authorities, allowed the Tongas to own firearms which certainly contributed to the near extermination of the rhino in the Northern Central Zambezi Valley and probably led to some poaching on the south bank.

The amount of disturbance and native hunting in the different regions of the Study Area, i. e. the human influence on the rhino abundance, may be expressed in terms of population indices giving the approximate number of Tongas per square mile along the south bank of the Zambezi. Where settlement had extended up the main tributaries, as along the Umniati, Bumi, and Sibilobilo rivers, the approximate length of occupied river bank has been included in the regional settlement index. The calculation of these indices has been based on population figures collected by COCKROFT (1949; and pers. comm.) and the mapping of native settlement by the Surveyor General of the former Federal Government of Rhodesia and Nyasaland.

The greatest average density of settlement in terms of available river frontage existed in the Sampakaruma chieftaincy, comprising of approximately 1750 people between Naodsa and Bumi rivers. In this area the Umniati and parts of the Zambezi valley (Fig. 3) were particularly heavily populated, yielding a mean population index of about 50 for Study Region I. The Mola chieftaincy, between the Bumi and Sengwa rivers, with approximately 1685 people, had almost as big a population as the Sampakaruma clan; but considering the available river valleys the average settlement was much less in this area. The greater part of Region III (Fig. 3) was very sparsely inhabited showing a population index of only 20–25. The Zambezi valley between Sengwa and Mwenda was occupied by several smaller chieftaincies totalling about 1000 people.

Distribution of the rhinoceros population in the Lake Kariba basin

Note: Total acreage: excludes 63 sq. miles unoccupied by rhinos between Study Regions (1 sq. mile = 259 ha = 2,59 k Population size: figures are population minimum, figures in brackets take rhino into account which may have been without being trapped (maximum population) Population density: a. Acreage considered to have been occupied by rhino: maximum population figure b. Acreage considered to have been occupied by rhino: minimum population figure c. Total acreage: minimum population figure (in regions II, IV, and VI some limited areas tainly not inhabited by rhino, have been deducted)	Population Total Population a. Density (in acres per b. one rhino) c.	Total juveniles & calves (Class II + III)	Total adults (Class I)	Age class III	Age class I Age class II	%ex	considered to have been occupied by rhinoceros	Total acreage	Regions of Study Area
Total acreage: excludes 63 sq. miles unoccupied by rhinos between Study Regions (1 sq. mile = 259 ha Population size: figures are population minimum, figures in brackets take rhino into account which may without being trapped (maximum population) Population density: a. Acreage considered to have been occupied by rhino: maximum population figure b. Acreage considered to have been occupied by rhino: minimum population figure c. Total acreage: minimum population figure (in regions II, IV, and VI some limitation) trainly not inhabited by rhino, have been deducted)	10 (to 12?) approx. 3,000 to 3,700 (to 5,200?)	4	6	1 1 -	2 4 -	03 +0 ••	36,900	52,400	ı
ccludes 63 sq. miles unoccupied by rhinos betw figures are population minimum, figures in bra without being trapped (maximum population) ty: a. Acreage considered to have been occupi b. Acreage considered to have been occupi c. Total acreage: minimum population fig tainly not inhabited by rhino, have bee	5 (to 6?) approx. 3,300 to 4,000 (to 5,700?)	1	4	i I	1 3 1 1 1 1.	0,3 +0 .0	20,000	40,200	11
noccupied by n minimum, d (maximum, lered to have lered to have minimum p abited by rh	22 (to 24?) approx. 2,700 to 3,000	7	15	2 - 2	96 -	↔ +0 ••	65,200	65,200	III
y rhinos bety figures in branches in branches in branches in branches in population for been occupe been occupe been occupe been occupendation figures.	I (to 4?) approx. ? 2,000 to 4,000 (to 6,000?)	1	р-1	i 	I I	· · · · · · · · · · · · · · · · · · ·	8,000 (a) 4,000 (b)	11,350	IV
s 63 sq. miles unoccupied by rhinos between Study F are population minimum, figures in brackets take rl at being trapped (maximum population) Acreage considered to have been occupied by rhino: Acreage considered to have been occupied by rhino: Total acreage: minimum population figure (in regional acreage: minimum population figure)	20 (to 25?) approx. 2,700 to 3,400	Сī	15	1 2 -	5 8 2	6.6.6.	67,100	67,100	1
Regions (1 schino into acchino into accinity accinity accinity accinity accinity according to the constant of the constant according to the constant	3 (to 5?) approx. 3,000 to 5,000	1	2	i 1	1 1 1	03 +0 •3	15,200	Section A. 15,200	
p. mile = 25 count which count which sopulation fipopulation find VI some	6 (to 8?) approx. 2,900 to 3,800	_	Œ	P	1 2 2	03 +0 •3	23,000	Section B. 23,000	
Total acreage: excludes 63 sq. miles unoccupied by rhinos between Study Regions (1 sq. mile = 259 ha = 2,59 km²) Population size: figures are population minimum, figures in brackets take rhino into account which may have been pushed onto mainland without being trapped (maximum population) Population density: a. Acreage considered to have been occupied by rhino: maximum population figure b. Acreage considered to have been occupied by rhino: minimum population figure c. Total acreage: minimum population figure (in regions II, IV, and VI some limited areas which were almost certainly not inhabited by rhino, have been deducted)	11 (to 13?) approx. 2,200 to 2,600	3	∞	1 1	3 1 5 1	O₃ +O •>	28,900	Section C. 28,900	
	4 (to 6?) approx. 2,000 to 3,000 (to 5,000?)	ı	4	1 1	3 1 1	03 +0 •2	12,000	33,300	IA
	62 (to 72?) approx. 2,900 to 3,400 (to 4,350?)	17	45	3 C 3 C 3 I	23 20 2	O ₃ +O	approx. 205,000 (321 sq. mils.)	approx. 270,000 (421 sq. mils.)	Total

The resulting average population index of 27 in Region V was intermediate to Regions

It is interesting to note that the rhinoceros density found in these three major regions was correspondingly highest in III, somewhat lower in V and definitely lowest in region I. Another correlation becomes evident when the areas of maximum settlement are determined. Such are found between region I and II with about 75, between III and IV with 40, and in VI with an index of 65–98. West of the Mwenda river the average index increases from above 50 to 100. All these concentrations are adjacent to those areas where no rhino were found (Fig. 3).

2. Local distribution within the regions seemed to be also dependant on water availability and vegetation. Areas with typical rhino habitat and plenty of water in pans between rivers, as for example in parts of Sengwa West V, were identical to those of

greatest rhino density.

Whether the destruction of all woody vegetation in incipient fishing grounds during 1958 to 1960 (Fig. 3) has influenced the rhino distribution permanently, was difficult to determine. Rhino tended to live along the edges of all these clearings. They seemed to need shade but fed out in them. Later the bush had regrown and rhino lived considerable time, for example, in the Bumi West clearing before the water trapped them there. The Sengwa West clearing may account for the fact that this section revealed less rhino than the other Sengwa sections.

Population Structure

The rhino trapped on islands at Kariba represented a segment of the population of the Central Zambezi Valley as a whole, whose distribution spread beyond the area affected by the Lake. There was no evidence to suggest that certain sex or age classes were more prone than others to becoming isolated, so that the 62 animals handled or recorded probably represented an unbiased sample of the whole population. As mentioned above, several animals drowned or died during attempts to rescue them and there were 4 which died of natural causes that may have been influenced by the overcrowded conditions on islands resulting from the concentration of game. This took place only after islands had been greatly reduced in size so that it was unlikely that the prevailing circumstances had caused a shift in the sex and age class composition of the sample trapped on islands, as the sample includes these natural deaths as well as rescue casualties.

In the present sample rhino were grouped into 3 age classes depending on their weights. Specimens under 600 lbs. were classed as calves and were probably not over one year old. Older sub-adults weighing 600 to 1600 lbs. were classed as juveniles. They were smaller than adults and were probably between one and 3½ years old. Rhino heavier than 1600 lbs., i. e. older than 3½ years were not distinguishable and termed "adult", although they were not necessarily all sexually mature. This classification, based on estimated weights, correlated with the general body proportions of the specimens handled and with the data on growth of rhino in captivity compiled by ROTH (unpublished). A source of possible error arose because of the difficulty of separating animals between 3 and 3½ years of age from adults when there were no adults with which to compare them. However, most juveniles were with adults and there were not more than 2 specimens in this category. These possible exceptions are taken into account when discussing the recruitment rate of this rhino population, but do not invalidate our conclusions, which in any case tend to be conservative and over-estimate the number of young reaching maturity.

The largest group of rhino of which we know was one of 8 individuals reported by

Cowles (1959); but this probably represented the temporary association of 2 or more parties, as most authors including Schater (1900), Fitzsimons (1920), Shortridge (1934), STOCKLEY (1950), STEVENSON-HAMILTON (1957), RIPLEY (1958), ANSELL (1960), and RITCHIE (1963) report them as solitary or associating in family groups of 2 or 3 animals. Even under the restricted conditions prevailing on islands at Kariba, groups did not coalesce. The social organization of 28 rhino was noted. These included 5 groups of 3, in 4 of which there was an adult male, adult female and calf or juvenile. In 2 of the 4 groups the juvenile had been weaned, although one female still had thin fluid in the udder, while in the other 2 groups she had a small calf. There were 2 pairs, a heavily lactating female and her calf and 2 mature males, which could not be separated until the one had been drugged, and even then it was necessary to drive the second away with a shot from a Verylight pistol. The remaining rhino, including 6 males and 3 females, were solitary. Two of the males and one of the females were not quite full grown, but at least 3 of the males and one of the females were old animals. An interesting observation involved an unweaned calf which escaped capture when its parents were removed from an island. It became closely associated with a solitary female with a dry undeveloped udder and the female showed no resentment of the association.

The only possible evidence of aggressiveness between rhino on islands was a juvenile male found dead with a big wound in its side, which may have been caused in a fight with another rhino. This was surprising under the restricted conditions on islands as 2 of 13 rhino introduced in 1962/63 into the Wankie National Park from Kariba were killed by previous inoculants from the same area (ROTH 1967). Both animals killed were females, one of which was a small juvenile, and there is a report from the Chizarira area of an adult female having been killed in the same way.

The sex and age class composition of the rhino found on islands is summarized by years in table 2. There was a total of 29 males, 28 females and 2 adults and 3 very small calves which could not be sexed, which suggests an adult and overall sex ratio approaching parity. There were 17 (27.4 per cent) which had not reached physical maturity.

Nine calves were trapped with 20 full grown females, a ratio of 45:100, although in annual samples the proportion of calves varied from 29 to 75:100. One female was trapped on 2 islands in successive years and had therefore to be taken into account

Table 2
Sex and ages of rhino caught in the Lake Kariba basin by years

Year Sample		Adult (age class I)			Juvenile (age class II)			Calf (age class III)				Calves: Ad. females:		
	ð	2	?	Т	ð	9	?	Т	ð	9	?	Т	Juveniles	
1959	2	1		1	2									
1960	8	3	3		6		1		1		1		1	33:100:33
1961	19	6	7		13	1	2		3		1	2	3	43:100:43
1962	17	9	3		121	1	1		2	2		1	3	752:100:66
1963	61	4	7	1	12	1	1		2	1	1		2	29:100:29
Total	62	23	20	2	45	3	5	0	8	3	3	3	9	45:100:40

¹ 2 adults marooned in 1962 were captured in 1963. — ² One female released in 1961 probably bred before being recaptured in 1962.

^{? =} sex unknown. T = total



Fig. 4. Transfer of immobilized rhino from sleigh onto raft for rescue from island (Photo: Wildlife Department, Salisbury)

when calculating both the 1961 and 1962 calf ratios, although she could not have contributed to the juveniles trapped in 1962.

The theoretical maximum reproductive potential of rhino was concluded from zoo breeding data compiled by ROTH (unpublished). Based on a 15½ to 16 month gestation period and a 12 day interval between calving and the first post partum oestrus, it is about 72–75 calves per 100 sexually mature females per year. Considering that sexual maturity is reached only, at about 4 years of age there may have been a number of full grown females in the present sample which were not sexually mature. There were 5 females classed as juveniles, i. e. between 1 and 3½ years old, so that if there was no differential mortality among sub-adults over one year old, there would have been 2 females between 3½ and 5 years of age. Present samples are small, but, as mortality is usually highest among younger age classes in wild populations, it is probable that at least 18 of the 20 adult-sized females were sexually mature. Thus the observed calving rate was 50:100 sexually mature females which is between 66 and 70 per cent of the theoretical potential.

If this potential was realized and there was no calf or juvenile mortality, there could be 180 to 188 juveniles between 1 and 3½ years old per 100 mature females in the population. At Kariba there were between 40 and 44.5 per 100 females depending on the proportion of sexually mature females in the sample of fully grown females. This is about 22 to 25 per cent of the maximum number theoretically possible. Thus 66 to 70 per cent of the maximum number of calves possible gave rise to 22 to 25 per cent of the theoretical maximum number of juveniles, which indicates about two thirds of the calves would have died before reaching adult size.

In this sample there were 8, or possibly 10 juveniles which were less than 31/2 years old. If these had included equal numbers of yearlings, two-year and three-year olds,

it would suggest that roughly 3 to 4 animals reached adult size each year. If the same number reached sexual maturity the annual replacement to the breeding herd would have been about 7 to 9 per cent adults or about 5 to 6 per cent of the total population; as there were approximately equal numbers of adult males and females. The discrepancy between the number of calves and juveniles, however, points to a high mortality among rhino early in life and the actual replacement was probably lower than these figures suggest. In fact the number of animals which proved difficult to distinguish as either adults or juveniles indicated an annual recruitment to the full grown segment of the population of less than 5 per cent.

Conclusions

Few population data are available from Black rhinoceros with which the results of this study could be compared. Furthermore, it is difficult to interpret meaningfully density figures of a population without relating these to the prevailing habitat conditions, and also without some knowledge of the species social and territorial behaviour. In this context it is interesting to note that KLINGEL and KLINGEL (1966) observed similar behaviour of rhinoceros in the Ngorongoro Crater to that recorded in the Lake Kariba basin. Almost equal numbers of males and females were distributed fairly evenly, in well defined home ranges, and most rhinoceros were solitary, or associated only temporarily in small groups of up to five. It was remarkable that this behaviour persisted under the crowded conditions on some islands at Kariba, and the lack of aggressiveness under these conditions led CHILD (1965) to question whether the species is truly territorial as HUTCHINSON and RIPLEY (1954) and RIPLEY (1958) have suggested.

If the distribution of rhino captured in the Lake Kariba basin is analysed in relation to the pattern of flooding it emerges that small groups lived in localised areas. probably river valleys, from which they were driven to higher ground by the rising waters. In these localities they probably each occupied less than an average of 3.4 sq. miles (8.9 km²), which compares with 2.9 sq. miles (7.5 km²) for each resident rhino (including calves) in the Ngorongoro Crater (KLINGEL and KLINGEL 1966), or the N. Aberdare National Park in Kenya for which BOURLIÈRE (1963) quoted the same average rhino density (52 rhino on 96,000 acres). KLINGELS' study showed that home ranges of rhino may overlap very considerably, and this may account for much greater lccal rhino densities, as observed, for example, by ROTH and WILSON (unpublished) in an area along the Sengwa river adjacent to the present study area. Here 38 rhino were captured for translocation to the Wankie National Park from a relatively well defined area of approximately 30 sq. miles, to give at an average less than 0.79 sq. miles (2.0 km²) per rhino. Deane (1964; pers. comm.) reported even an overall density of 3.4 rhino per sq. mile, with concentrations of up to 5.6 animals per sq. miles (i. e. 0.2—0.3 sq. miles or 0.5-0.8 km² per rhino) in the Hluhluwe Game Reserve in Natal. In both of the areas, however, there was clear evidence of over-utilization of habitats, and overpopulation in Hluhluwe is thought to have been the main cause for a large die-off in 1961. The optimum home range is probably much larger than these figures would indicate, and in any case the local density of a healthy rhino population will fluctuate according to prevailing ecological conditions.

The overall population density in the study area, of one rhino per 6.8–7.8 sq. miles (~ 18–20 km²), was lower than any of the density figures recorded from defined localities within this area. This suggests that large parts of the studied area of the Lake Kariba basin were unoccupied by this spezies. As far as could be ascertained during the rescue operations and from earlier aerial photos, topography and vegetational con-

ditions may have accounted for the absence of rhino from some areas, but in most of the study area suitable habitat was available, including those parts in which no rhino were caught (Fig. 3). The recorded overall abundance of rhino may therefore be considered relatively low; especially if compared with other adiacent areas, as for example east of the Umniati river, where one Tsetse Control hunter alone reported shooting over 60 rhinoceros in about 2 years (ROTH 1967). The present study shows that human settelement had apparently influenced the general distribution and abundance of rhino in the Lake Kariba basin. Considering that the study area was relatively sparsely populated compared with many other areas in Africa where there are Black rhinoceros, and that the inhabitants were chiefly agriculturists, the inverse correlation between disturbance and hunting intensity and distribution of rhino demonstrates how sensitive such a population can be to even light hunting, and how easily the species can be shot out in an organized campaign.

In this context it is relevant to evaluate the rate of reproduction and turnover of the studied population. The observed calving rate of 50 calves per 100 mature females per year was higher than that recorded by KLINGEL and KLINGEL (1966) for the Ngoronsoro rhino population, but was followed by a high juvenile mortality. The calculated annual replacement rate of ≤ 5 per cent to the full grown segment of the population would thus have to be considered low, although the net annual increase under normal conditions has been estimated at only 5-8 per cent (SIMON 1966). Maintenance of rhinoceros populations would appear to be largely dependant upon the longevity of the adults, and this would explain the ease with which the species can be eleminated by hunting. It also highlights the danger to its survival where it is in conflict with man or does not receive adequate effective protection from even relatively light exploitation.

Summary

Rescue operations during the flooding of Lake Kariba in Rhodesia from 1959 to 1963 were used to study the distribution and population structure of Black rhinoceros (Diceros bicornis L.) in a section (484 sq. miles or 1254 km²) of the south bank of the Central Zambezi Valley.

1. The rhino trapped on islands were considered to represent an unbiased sample of a larger rhinoceros population whose distribution spread beyond the flooded area. The sex ratio in the sample approached parity and rhinoceros lived either solitarily or in small groups. Even

under the restricted conditions prevailing on islands, groups did not coalesce.

2. 62 rhinoceros were distributed over approximately 321 sq. miles (831 km²) with a maximum local population density of less than 3.4 sq. miles (8,9 km²) per each animal. This figure is compared with records from other areas, and its relation to the size of home range in this

species is discussed.

3. Considering the relative uniformity of the available habitat the overall population density for the whole area, of one rhino per 6.8-7.8 sq. miles (~ 18-20 km²) was considered to be low. The marked difference between local and overall densities suggested that large areas were unoccupied by rhinoceros, and human settlement apparently had influenced the

general distribution and abundance.

4. With a calving rate of 50:100 sexually mature females the reproduction was 66-70% of the theoretical maximum potential as concluded from zoo breeding data. An analysis of the age structure in conjunction with field observations indicated, however, a high youth mortality reducing the annual replacement rate to about 5%. Maintenance of rhinoceros populations appears to be largely dependant upon the longevity of the adults.

Acknowledgements

The cooperative support given to this study by Mr. D. LOVEMORE, Chief Entomologist, Tsetse Control Branch, Department of Veterinary Services, and Mr. R. Fothergill, Wildlife Officer in charge of the Lake Kariba rescue operations, formerly Department of Wildlife Conservation, Rhodesia, and their staff is gratefully acknowledged. In particular we wish to thank Mr. R. PILSON of the Tsetse Control Branch, for his valuable advice and assistance in the cartographic work of this study.

Zusammenfassung

Rettungsmaßnahmen während der Anstauung des Kariba-Sees in Rhodesien von 1959 bis 1963 wurden benutzt, um die Verteilung und Populationsstruktur von Spitzmaul-Nashörnern (Diceros bicornis L.) in einem Abschnitt von 1254 gkm auf der südlichen Seite des Sambesi zu

- 1. Die auf Inseln festgehaltenen und von dort evakuierten Nashörner wurden als repräsentativ angesehen für eine über das überflutete Gebiet hinaus verbreitete größere Nashorn-Population. Das Geschlechterverhältnis in dem untersuchten Populationsanteil war nahezu gleich, und die Nashörner lebten entweder einzeln oder in kleinen Gruppen. Nicht einmal unter den eingeengten Verhältnissen auf Inseln schlossen sich diese Gruppen zusammen.
- 2. 62 Nashörner waren über rund 831 qkm. verbreitet mit einer örtlichen maximalen Populationsdichte von weniger als 8,9 qkm pro Tier. Diese Zahl wird mit Angaben aus anderen Gebieten verglichen und ihre Beziehung zu der Reviergröße bei Nashörnern erörtert.
- 3. Berücksichtigte man, daß die Biotopverhältnisse relativ einheitlich waren, erschien die mittlere Populationsdichte für das gesamte untersuchte Gebiet, von einem Nashorn pro 18 bis 20 qkm gering. Der ausgeprägte Unterschied zwischen örtlicher und Gesamt-Populationsdichte ließ erkennen, daß größere Gebiete nicht von Nashörnern besetzt waren; menschliche Siedlung hatte die Verteilung und das allgemeine Vorkommen offensichtlich beeinflußt.
- 4. Mit einer Geburtsrate von 50 saugenden Jungtieren pro 100 geschlechtsreifer Nashorn-Kühe lag die Vermehrung der Population bei 66-70 % der von Zoo-Zuchtdaten abgeleiteten theoretischen Höchst-Vermehrungsrate. Eine Analyse der Altersstruktur, in Verbindung mit Feldbeobachtungen, ergab jedoch eine hohe Jugendmortalität, wodurch sich der jährliche Zuwachs erwachsener Tiere in der Population auf ungefähr 5 % verminderte. Die Erhaltung von Nashornpopulationen scheint stark abhängig zu sein von der Lebensdauer der Zuchttiere.

References

- Ansell, W. F. H. (1959): Further Data on the Northern Rhodesian Ungulates. Mammalia 23, 332-349.
- (1960): Mammals of Northern Rhodesia. Government Printer, Lusaka; 155 pp.
- CHILD, G. (1965): The behaviour of large mammals during the formation of Lake Kariba.
- Cape Town University; Thesis; 140 pp.
 CHILD, G., and FOTHERGILL, R. (1962): Techniques used to rescue Black Rhinoceros (Diceros bicornis) on Lake Kariba, Southern Rhodesia. Kariba Studies. Manchester University Press;
- CHILD, G., and SAVORY, C. R. (1964): The Distribution of Large Mammal Species in Southern Rhodesia. Arnoldia (Rhodesia) 1, No. 14; 1-15.
- COCKCROFT (1949): Removal of Natives Consequent upon the Kariba Gorge Hydro-electric Power Scheme — Scientific Research. Unpubl. report; Min. Native Affairs; Govt. South. Rhodesia; Salisbury; 26 Nov. 1949.
- Cowles, R. B. (1959): Zulu Journal. Univ. Calif. Press, Berkeley.
- HARTHOORN, A. M. (1962): Atractic, hypnotic and narcotic mixtures for the capture and handling of large wild animals. Brit. vet. J. 119, 42-63.
- HARTHOORN, A. M., and LOCK, J. A. (1960): The rescue of rhinoceroses at Kariba Dam. Oryx, London; 5 (6), 352—355.
- HARTHOORN, A. M., and Player, I. C. (1964): The Narcosis of the White Rhinoceros: A Series of Eighteen Case Histories. Proc. V Intern. Symp. Dis. Zoo Anim. Tijd. Diergenesk. 89, Suppl. 1, 225—229.
- Fitzsimons, F. W. (1920): The Natural History of South Africa. Vol. 2. London; 4 vols.
- KLINGEL, H. and U. (1966): The rhinoceroses of Ngorongoro Crater. Oryx, London; 8 (5), 302-306.
- HUTCHINSON, G. E., and RIPLEY, S. D. (1954): Gene dispersal and the ethology of the rhinocerotidae. Evolution 8, 178-179.
- RIPLEY, S. D. (1958): Comments on the Black and Square-lipped Rhinoceros species in Africa. Ecology 39, 172-174.
- RITCHIE, A. T. A. (1963): The black Rhinoceros (Diceros bicornis). E. Afr. Wildl. J. 1, 54-62, Rотн, H. H. (1967): White and Black Rhinoceros in Rhodesia. Oryx, London; 9 (3), 217—231.
- Scudder, T. (1962): The Ecology of the Gwembe Tonga. Manchester University Press; 224 pp. SCLATER, W. L. (1900): Mammals of South Africa. Vol. 1. London; 2 vols; 324 pp.
- SHORTRIDGE, G. C. (1934): The Mammals of Southwest Africa London; 2 vols; 729 pp.
- Stevenson-Hamilton, J. (1947): Wildlife in South Africa. London; 400 pp.
- STOCKLEY, C. H. (1950): The Hook-lipped Rhinoceros. Zoolife 5 (3), 88-91.

BOURLIÉRE, F. (1963): Standing-crop biomass of wild ungulate populations in various African habitats. Discussion of paper presented at Symp. Afr. Mammals, September 1963, Salisbury. SIMON. N. (1966): Red Data Book; Vol. I: Mammalia — a compilation. IUCN Morges.

Authors' addresses: Dr. Dr. Harald H. Roth, Wildlife Officer FAO Roma, Italy, and Dr. Graham Child, FAO Wildlife Ecologist, Game Department, Gaberones, Botswana

Nabelschnur-Längen bei Insektivoren und Primaten¹

Von W. B. SPATZ

Max-Planck-Institut für Hirnforschung, Neuroanatomische Abteilung, Primatologie, Frankfurt/Main — Direktor: Prof. Dr. R. Hassler

Eingang des Ms. 27, 9, 1967

Trotz der ungemein reichhaltigen und vielseitigen Literatur über Säugetiere wissen wir heute noch relativ wenig über deren Nabelschnur. Während der gerade für diese Wirbeltierklasse so bedeutsamen Zeit der intrauterinen Entwicklung spielt die Nabelschnur, die "Lebensader" des sich entwickelnden Foeten, eine bedeutsame Rolle.

Vor allem durch die Untersuchungen von SLIJPER (1936, 1960), DE SNOO (1942) und STARCK (1957) ist bekannt, daß die Länge dieses Stranges bei verschiedenen Säugergruppen außerordentlich unterschiedlich sein kann. Das insgesamt vorliegende Material ist aber noch derart lückenhaft, daß kaum befriedigende Aussagen über Ursachen und Bedeutung der Länge der Nabelschnur gemacht werden können, ebenso wenig über innerartliche Variabilität und über Veränderungen der relativen Nabelschnurlänge (= Nabelschnurlänge [NL] in % der Scheitel-Steiß-Länge [SSL] des Foeten) während der Ontogenese.

Besonders für Insektivoren und Primaten liegen – mit Ausnahme einzelner Formen wie Pan und Homo – nur wenige Daten vor. Obwohl vor allem die Primaten immer mehr in das Interesse der Forschung rücken und in zunehmendem Maße auch in Gefangenschaft gezüchtet werden, gelangen praenatale Entwicklungsstadien immer noch selten zur Untersuchung. Die Angabe weiterer Daten erscheint somit gerechtfertigt,

auch wenn sie bei Weitem noch keine endgültigen Aussagen gestatten.

In Tabelle 1 habe ich alle mir aus der Literatur zur Kenntnis gelangten sowie eigene Angaben, Insektivoren und Primaten betreffend, zusammengestellt. Obwohl die Länge der Nabelschnur hauptsächlich beim Geburtsakt eine möglicherweise entscheidende Bedeutung hat, sind auch alle mir bekannten jüngeren Stadien mitberücksichtigt, da Relationsverschiebungen während der Ontogenese von zumindest theoretischem Interesse sind. Tabelle 2 zeigt die aus Tabelle 1 errechneten Durchschnittswerte, für engere Gruppen oder auch Gattungen. Der besseren Übersicht wegen sind auch Einzelwerte (Daubentonia, Galago) nochmals aufgeführt.

STARCK (1957) bezeichnet relative Nabelschnurlängen bis zu 30% der SSL des Foeten als kurz, Werte ab 75% als lang. Mit Recht betont er, daß der Reifegrad und

¹ Herrn Dr. H. Stephan danke ich besonders für die Überlassung des wertvollen Materials madagassischer Insektivoren sowie für Gewichtsangaben adulter Tiere.